

## INFLUENCE OF FORAGING AND ROOSTING BEHAVIOR ON HOME-RANGE SIZE AND MOVEMENT PATTERNS OF SAVANNAH SPARROWS WINTERING IN SOUTH TEXAS

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**ABSTRACT.**—We used radio telemetry to examine Savannah Sparrow (*Passerculus sandwichensis*) home-range size and foraging and roosting behavior on Padre Island National Seashore in south Texas during January and February, 2002 and 2003. Savannah Sparrows maintained fixed home ranges in winter. Mean home-range size (95% Kernel Home Range [KHR]) was 9.1 ha with a mean core area (50% KHR) of 0.9 ha. Within home ranges, mean foraging and roosting areas were 5.6 and 6.6 ha, respectively. Three distinct habitat types were used by Savannah Sparrows on the island: foredunes (adjacent to the ocean), interior grasslands, and lagoons. Birds using the foredunes had significantly larger home ranges and traveled longer distances between their foraging and roosting locations, always moving inland to roost. Roosting and foraging areas overlapped less for these birds (20%) compared with the overlap for birds found in interior grasslands (45%) and lagoons (55%). The greater distance traveled to roost sites by birds foraging in the foredune habitat appeared to be related to increased exposure in that habitat type. Savannah Sparrows selected foraging areas with less vegetative biomass and more bare ground than random sites. Roost sites had greater total (live) cover than foraging and random sites. Savannah Sparrows foraged alone or in loose aggregations with conspecifics. Birds roosted alone or in aggregations of up to 30 individuals. Savannah Sparrows often roost outside of their foraging areas; this study draws attention to differences in space use for roosting and foraging Savannah Sparrows. Although Savannah Sparrows maintained relatively small home ranges, they occasionally moved at larger spatial scales, suggesting a need for intact grassland patches much larger than the average home-range size. Received 18 February 2004, accepted 6 December 2004.

The relationship among foraging- and roost-site selection, behavior, and home-range size is not well understood for non-breeding emberizid sparrows. This is related, in part, to the small size, cryptic coloration, and nomadic nature of some members of this group. The degree of nomadic behavior varies among species and possibly within and among regions (Gordon 2000). In Arizona, where seed abundance can vary substantially among patches and winters, Gordon (2000) found that four species of emberizid sparrows all tended to occupy fixed home ranges during the winter period, with the Savannah Sparrow (*Passerculus sandwichensis*) exhibiting the greatest variation in movement patterns. Gordon (2000) found that local movement patterns of Savannah Sparrows differed between study sites.

There is little evidence of Savannah Sparrow fidelity to wintering grounds, and movement patterns appear to be variable (Odum

and Hight 1957, Wheelwright and Rising 1993, Gordon 2000, Ginter 2004). Understanding factors that contribute to variation in the extent of this sparrow's movements is important for its management and conservation on wintering grounds. Using flush-netting techniques, Odum and Hight (1957) found that winter home-range sizes in Georgia varied from 6 to 60 ha. Gordon (2000) did not estimate home-range sizes, but found that Savannah Sparrows in southeastern Arizona tended to remain within a fixed home range and moved an average distance of 186 m between consecutive locations. Using flush-netting, Gordon (2000) detected sedentary behavior at one site and high mobility at another. Intraspecific differences in behavior may result in variation in response to capture using flush-netting (Gordon 2000, Ginter 2004). Radio-telemetry may provide a better estimate of movement patterns and the degree of sedentary behavior.

Variation in movement patterns may be related to the distribution of seed resources across the landscape, predator avoidance, or the distribution of suitable foraging and roosting habitat. Other studies have found winter sparrow abundance to be correlated with seed

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production, suggesting that sparrows track resource abundance (Pulliam and Parker 1979, Grzybowski 1982). Unlike more sedentary grassland sparrows, such as Grasshopper (*Ammodramus savannarum*), Baird's (*A. bairdii*), Henslow's (*A. henslowii*), and Cassin's sparrows (*Aimophila cassinii*) that forage within dense grass cover (Pulliam and Mills 1977, Plentovich et al. 1999, Gordon 2000, Carrie et al. 2002), Savannah Sparrows have been observed to forage in open areas with little cover (Grzybowski 1982, Lima 1990, Lima and Valone 1991). Lima and Valone (1991) suggest that predator avoidance is an important aspect of foraging-site selection for grassland sparrows. Through experimental manipulation, they found that the availability of cover changes the composition of the winter avian community. Savannah Sparrows seem to forage within a matrix of open areas and denser cover (Watts 1991). Although little is known of Savannah Sparrow roost-site selection, most avian species are thought to select winter roost sites with greater vegetative cover due to enhanced microclimate and predator protection (Walsberg and King 1980, Buttemer 1985). We hypothesized that Savannah Sparrow foraging and roosting habitats would differ, and that the distribution of these habitats would contribute to variation in movement patterns. Movement patterns may also be related to seed abundance and we predicted that home-range size would be inversely correlated with seed abundance and biomass.

#### METHODS

*Study area.*—We conducted our study along the Texas coast on Padre Island National Seashore. North Padre Island is a long, narrow barrier island approximately 120 × 4 km (Wiese and White 1980), and is characterized by strong, moisture-laden gulf winds (Drawe et al. 1981). Winter temperatures rarely drop below freezing (Drawe and Kattner 1978). Unlike other coastal barrier islands in the Gulf of Mexico, Padre Island has a distinct grassland component; woody vegetation accounts for less than 0.2% of the plant community (Negrete et al. 1999). The interior grasslands are dominated by little bluestem (*Schizachyrium scoparium littorale*), gulfdune paspalum (*Paspalum monostachyum*), and bushy bluestem (*Andropogon glomeratus*). Upland dune

habitats are characterized by seaoats (*Uniola paniculata*), beach morning-glory (*Ipomoea imperati*), and partridge pea (*Chamaecrista fasciculata*). Dominant plants found in and adjacent to freshwater marshes are gulf cordgrass (*Spartina patens*), bulrush (*Scirpus pungens*), and spikerush (*Eleocharis flavescens*). Primary plants in saltwater marshes are halophytic, including shoregrass (*Monanthochloë littoralis*), saltgrass (*Distichlis spicata*), glasswort (*Salicornia bigelovii*), beachwort (*Batis maritima*), and sea-ox-eye (*Borrchia frutescens*) (Hatch et al. 1999).

*Radio telemetry.*—We captured birds in mist nets at 7 sites in 2002 and 11 sites in 2003 across the northern 32- × 4-km section of the island. Radio transmitters were placed on 57 Savannah Sparrows during January and February of 2002 and 2003 (21 in 2002 and 36 in 2003). We fitted birds with 0.72-g BD-2 transmitters (Holohil Systems, Ontario, Canada; 4.0–4.5% of body weight; mean life span = 26.6 days ± 0.9 SE, range = 21–37 days). We attached transmitters using the leg-back harness technique (Rappole and Tipton 1991). Harness fit was evaluated for each bird prior to release by placing the bird in an enclosure and observing its movements. If a bird's movements were restricted, the transmitter was removed and the bird was released (C. E. Gordon pers. comm.).

Initially, we attempted collecting data at a minimum of four foraging and three roosting locations per week for each bird; however, in 2003 we increased the number of locations because our 2002 data were insufficient for analyzing home-range sizes of most birds. Data on foraging locations were collected between 07:00 and 17:00 CST, whereas data on roost-site selection were collected between 20:00 and 05:00. We located most birds visually. If a bird appeared to respond to the observer's presence before being observed, we used the strength of the radio signal to mark its initial position (Vega Rivera et al. 2003). For each radio-tagged Savannah Sparrow, we recorded whether it was solitary or found in a flock, and we recorded whether the flocks were single- or mixed-species flocks. We did not record the number of individuals within flocks due to difficulty in determining flock membership. Roosting Savannah Sparrows remained stationary when approached and we

tried to avoid flushing them. If we flushed a radio-tagged sparrow from its roost site, we recorded the number of individuals in close proximity (within a 2-m radius) to the radio-tagged bird. All locations where birds were first observed were marked in UTM coordinates with handheld Garmin GPS units.

We examined Savannah Sparrow use of three distinct habitat types within specific geographic areas on the island: (1) foredunes, which separate the beach front from the interior habitats; (2) interior grasslands; and (3) the edge of the lagoon (Laguna Madre). We classified radio-tagged Savannah Sparrows by habitat type and calculated foraging and roosting areas for each habitat. We calculated the distance from the center of the bird's estimated foraging area to each nocturnal roost location to determine the mean distance traveled between foraging and roost sites. We also calculated the percentage of the roosting home range that overlapped with the foraging area.

*Habitat measurements.*—Over the two winters, we measured the structural characteristics of the vegetation at five randomly selected foraging locations per bird ( $n = 46$  Savannah Sparrows), five roosting locations per bird ( $n = 44$  Savannah Sparrows), and at paired random points. Random locations were selected by choosing a random azimuth (0–360°) and a random distance between 0 and 50 m; we used the foraging and roosting locations as center points and the algorithm suggested by Skalski (1987) to correct for bias when sampling in circular plots. A visual obstruction reading (VOR, an index of vegetation biomass), was taken using a Robel pole at each location with four readings per point (Robel et al. 1970). A Daubenmire frame (20 × 50 cm) was used to estimate percent grass, forb, litter, woody, and total (all live vegetation) cover and bare ground (Daubenmire 1959). We measured maximum height of grass and forbs (the tallest plant in each frame) and the depth of horizontal vegetation within the Daubenmire frame (Desmond 2004).

In 2003, we quantified seed abundance and biomass by collecting surface soil samples at 10 foraging locations and 10 randomly selected paired points for nine Savannah Sparrows selected randomly from our radio-tagged birds. Random points were selected using the same criteria outlined above. We collected

four subsamples at each location and each random point. The four subsamples were chosen randomly from within a 1-m radius. We placed an 8.6-cm-diameter metal hoop on the ground and scooped the soil from inside the hoop to a depth of 0.8 cm for a total of  $46.4 \times 4 \text{ cm}^3$  of soil per sample. This technique is a modification of the method used by Grzybowski (1982). Samples were placed in labeled bags and dried at 50° C for approximately 24–48 hr.

To analyze seed samples, a hydropneumatic root elutriator was used to separate inorganic from organic material (Gross and Renner 1989). Seeds were separated from the remaining organic material using tweezers and a 10× magnification microscope (Pulliam and Brand 1975). Seeds were identified to genus, and, when possible, to species. For each sample, seeds were counted and weighed to the nearest one-thousandth of a gram. Seeds >5 mm in length or width were not included in the analyses.

*Data analyses.*—We used a non-parametric Kernel Home Range (KHR) estimator to determine the size of the home range for each bird; the KHR estimates the minimum area in which a Savannah Sparrow had a specific probability of being located (Worton 1995, Seaman and Powell 1996). We calculated a fixed KHR at 50% (core area) and 95%, and calculated smoothing parameters using least squares cross-validation (Seaman and Powell 1996, Hooze and Eichenlaub 1997). Cross-validated fixed-kernel home ranges have been found to be the most accurate of the home-range estimators (Seaman and Powell 1996). We used the ANIMAL MOVEMENTS extension program for ArcView 3.2 to perform calculations of the 50% and 95% KHR estimates (Hooze and Eichenlaub 1997). KHR estimates were calculated separately for foraging and roosting locations, and all locations combined (combined home range). Consecutive locations for individual sparrows were separated by a minimum of 12 hr and we used only those birds for which we had  $\geq 20$  telemetry locations. This resulted in  $\geq 20$  locations for foraging areas and combined home-range sizes but fewer (mean = 13) for roosting areas. However, the standard errors for foraging- and roosting-area estimates were similar and we believe the data provided a good estimate of

TABLE 1. Mean and range (ha) of winter home-range size, foraging area, roosting area, and core foraging area, and number of telemetry locations (SE) for Savannah Sparrows ( $n = 28$ ) on Padre Island National Seashore, Texas, during January and February, 2002 and 2003. Home ranges and foraging and roosting areas were calculated using a 95% Kernel Home Range (KHR) estimator; a 50% core estimator was used for core foraging areas.

Area estimated	Size (SE)	Range in area	No. telemetry locations
95% KHR			
Home range	9.1 (1.8)	0.2–31.7	35 (1.8)
Foraging area	5.6 (0.8)	1.0–19.8	22 (1.2)
Roosting area	6.6 (1.0)	0.4–17.9	13 (0.8)
50% KHR			
Core foraging area	0.9 (0.2)	0.9–4.1	22 (1.2)

roosting patterns (Table 1). Each bird was followed until the transmitter battery died, the bird lost its transmitter, the signal disappeared, or there was a confirmed mortality.

A Kruskal-Wallis test was used to examine, by habitat type, size differences in foraging areas, roosting areas, and home-ranges. We also compared mean distance traveled between foraging and roosting sites and tested for differences in percentage overlap between roosting and foraging areas among the three habitat types. For all Kruskal-Wallis tests we report the exact chi-square. All statistical analyses were performed using SAS 8.02 (SAS Institute, Inc. 1990).

Vegetation associations were evaluated by comparing foraging and roosting locations with each other and with paired randomly selected points; we used paired *t*-tests to analyze these data. We performed Shapiro-Wilkes tests to determine whether variables were normally distributed. When appropriate, we transformed data using a square-root transformation. To adjust for significance when performing multiple tests, we used the sequential Bonferroni correction (Rice 1989). We used Spearman rank correlation to test for a relationship between seed abundance and size of the 95% foraging KHR. Home-range sizes and vegetation characteristics are reported as means  $\pm$  SE.

## RESULTS

Of 57 Savannah Sparrows fitted with transmitters, we had a sufficient number of locations to calculate home-range size for 28 birds. With the exception of four birds discussed below, the birds excluded from analyses were those that died, slipped their trans-

mitters, or for which we had insufficient data (in 2002). There were three confirmed mortalities in 2002 and five in 2003. Because we detected no differences in between-year home-range sizes, we combined data from the two winters. The mean home-range size (95% KHR) was 9.1 ha and mean foraging and roosting areas were 5.6 and 6.6 ha, respectively; the mean core foraging area (50% KHR) was 0.9 ha (Table 1). We had difficulty locating four birds: two disappeared and two exhibited large-scale movement. One sparrow moved to a site approximately 2 km from its point of capture, where it remained for 5 days before returning and then permanently disappearing. A second bird moved 800 m from its point of capture, where it remained until it lost its transmitter 6 days later. Each radio-tagged sparrow foraged within a flock on at least one occasion. When foraging in flocks, Savannah Sparrows always foraged with conspecifics in loose aggregations (birds 1–10 m apart but apparently in vocal communication). We observed a mean of  $1.3 \pm 0.4$  ( $n = 43$ ) sparrows roosting within approximately 2 m of radio-tagged Savannah Sparrows. Although we suspect that radio-tagged Savannah Sparrows were roosting only with conspecifics, this could not be confirmed due to the difficulty of identifying them at night.

There were no detectable differences in sizes of foraging and roosting areas among birds using foredune, lagoon, and interior habitats ( $\chi^2_{\text{foraging}} = 1.38$ ,  $df = 2$ ,  $P = 0.50$ ;  $\chi^2_{\text{roosting}} = 5.15$ ,  $df = 2$ ,  $P = 0.081$ ; Table 2). Home-range size did differ among the three habitat types ( $\chi^2 = 8.73$ ,  $df = 2$ ,  $P = 0.010$ ; Table 2); mean home-range size of sparrows using the foredune habitat was larger than that of

TABLE 2. Kernel Home Range (95%) size (SE) for Savannah Sparrows, by habitat type, on Padre Island National Seashore, Texas, during January and February, 2002 and 2003. Different letters within columns denote significant between-habitat differences (Kruskal-Wallis test:  $P \leq 0.05$ ).

Habitat (n)	Home range (ha)	No. locations	Foraging area (ha)	No. locations	Roosting area (ha)	No. locations
Foredune (7)	16.6 (3.3) A	34.0 (4.5)	5.7 (1.3) A	21.9 (3.1)	9.9 (1.4) A	12.1 (1.5)
Grassland (13)	7.0 (1.6) B	33.2 (2.5)	6.1 (1.0) A	20.8 (1.5)	10.0 (4.6) A	12.4 (1.1)
Laguna Madre (8)	5.9 (1.7) B	41.2 (3.6)	4.4 (1.0) A	25.0 (2.0)	5.7 (1.8) A	16.2 (1.7)

sparrows using the other two habitat types. The mean distance traveled between the center of the estimated foraging areas and roosting locations differed among the three habitat types ( $\chi^2 = 10.29$ ,  $df = 2$ ,  $P = 0.026$ ). Sparrows using foredune habitat traveled farther between the centers of their foraging areas and roosting locations (mean = 337 m) than birds using interior grasslands (mean = 108 m) or lagoons (mean = 107 m). The percentage of overlap between roosting and foraging areas differed among the three habitat types ( $\chi^2 = 7.43$ ,  $df = 2$ ,  $P = 0.020$ ). Overlap for sparrows using foredune habitat was minimal (20%), whereas it was 45 and 55% for birds using interior grassland or lagoon habitats, respectively (Fig. 1). For example, there was no overlap of roosting and foraging areas for bird #279, but some birds using interior grassland and lagoon habitats had roosting areas completely contained within the foraging area (#840) or vice versa (#71); others had some overlap, but also maintained distinct foraging and roosting areas (#959).

Foraging areas had more bare ground and less VOR and horizontal depth than randomly selected points. When compared with roosting sites, foraging sites had more bare ground, less total cover, and lower horizontal depth. Roost sites had greater total cover and grass cover than randomly selected sites (Table 3).

Seed biomass did not differ between foraging and random sites and was positively correlated with the size of the 95% foraging KHR (Spearman rank correlation:  $r = 0.68$ ,  $P = 0.042$ ). On the other hand, seed abundance was significantly greater in samples collected at foraging sites compared with random sites (Wilcoxon-Mann-Whitney  $U$ -test = 62.5,  $P = 0.043$ ). There was no relationship between seed abundance at foraging sites and size of the 95% foraging KHR (Spearman rank correlation:  $r = 0.28$ ,  $P = 0.46$ ). Seed biomass

and abundance included seeds of all shapes and sizes that could be reasonably consumed by Savannah Sparrows; seeds  $>5$  mm in width or diameter were excluded from the analyses. The most common seed species were present at both foraging and random locations and included little bluestem, *Cyperus* spp., *Eleocharis* spp., camphorweed (*Heterotheca subaxillaris*), *Dichanthelium* spp., *Paspalum* spp., fall witchgrass (*Digitaria cognata*), and panicgrass (*Panicum amarum*).

## DISCUSSION

Savannah Sparrows exhibited strong sedentary behavior within winters; the majority of their foraging movements were restricted to an average core area of approximately 1 ha. The scale of movement detected in this study was smaller than previously estimated. However, we did observe extremes in home-range size ranging from 0.15 to 31.7 ha. We also observed large-scale movements of two Savannah Sparrows not included in the home-range analyses, with one moving as far as 2 km from its point of capture. Two radio-tagged sparrows disappeared altogether from the study area. Using a flush-netting technique, Gordon (2000) recaptured 3.8% (within winters) of the Savannah Sparrows banded on 7-ha plots, but had much higher recapture rates for Baird's, Grasshopper, Vesper (*Pooecetes gramineus*), and Cassin's sparrows. The low recapture rate for Savannah Sparrows in Arizona may indicate that the average winter home-range size is larger there than it is in coastal south Texas, or it may indicate that radio telemetry is a more reliable method for estimating home-range size and the degree of sedentary behavior for this species. Our study is the first to use radio telemetry to estimate winter home-range size for Savannah Sparrows. The small, average home-range size in south Texas may indicate a reliable resource

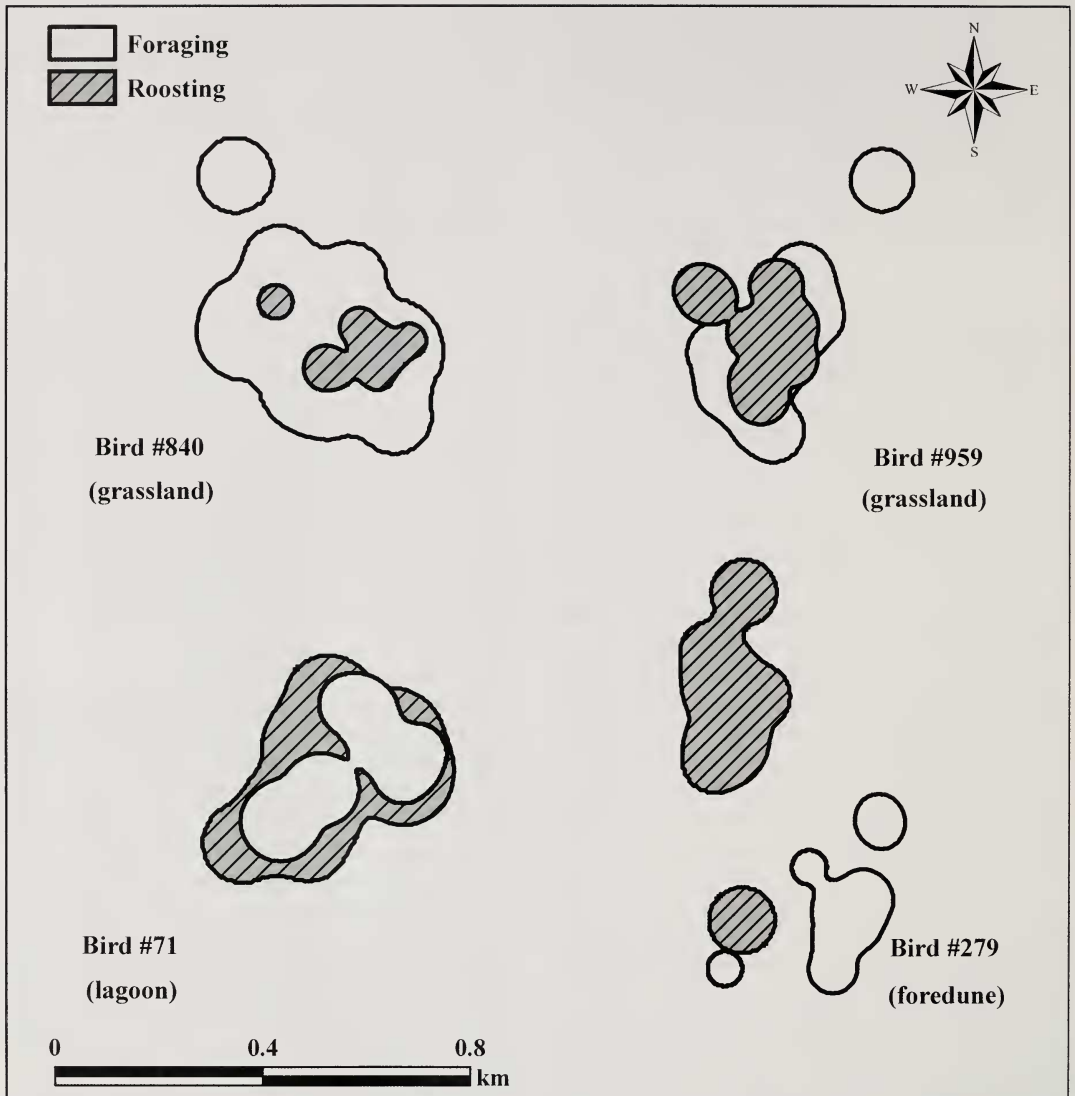


FIG. 1. Examples of distribution of foraging and roosting areas within home ranges of four Savannah Sparrows wintering on Padre Island National Seashore, Texas, January and February, 2002 and 2003. The roosting area of bird #840 (interior grasslands habitat) was 100% contained within its foraging area; 71% of the roosting area of bird #959 (interior grasslands habitat) was contained within its foraging area; 100% of the foraging area of bird #71 fell within its roosting area. There was no overlap between roosting and foraging areas of bird #279 (foredune habitat).

base to maintain sparrows within a small area throughout the winter period. Alternatively, Savannah Sparrows may tend to occupy relatively small areas (1 ha) for short periods of time (1–2 months), but may occasionally wander at larger spatial scales during the course of the winter (November–March). This could explain the large-scale movement we ob-

served for two sparrows in this study, and the high degree of variability in recapture rates between sites in Arizona (Gordon 2000).

Movement patterns between roosting and foraging sites have not been previously reported for wintering Savannah Sparrows. The mean distance moved from the center of foraging areas to roosting sites was 165 m, with

TABLE 3. Comparisons of mean vegetative structure at foraging, random, and roosting areas within Savannah Sparrow home ranges during January and February, 2002 and 2003 on Padre Island National Seashore, Texas. Asterisks denote significant differences (paired *t*-test:  $P \leq 0.05$ ) between paired locations.

Variable	Foraging versus random areas (SE)		Roosting versus random areas (SE)		Foraging versus roosting areas (SE)	
	Foraging	Random	Roosting	Random	Foraging	Roosting
% Grass	66.2 (3.3)	59.1 (3.0)	76.9 (3.3)*	62.7 (3.4)*	68.9 (3.3)	69.0 (3.7)
% Forb	24.9 (3.0)	32.1 (2.8)	21.6 (3.3)	25.2 (2.5)	22.8 (3.0)	27.7 (3.7)
% Bare ground	41.7 (2.2)*	31.2 (2.1)*	30.6 (2.5)	35.8 (2.7)	41.8 (2.2)*	32.2 (2.2)*
% Leaf litter	8.1 (1.7)	7.4 (1.7)	4.1 (0.7)	8.5 (2.0)	7.7 (1.7)	6.0 (1.2)
% Total cover <sup>a</sup>	50.8 (2.0)	58.5 (2.4)	65.3 (2.2)*	53.8 (2.9)*	50.6 (2.0)*	61.8 (2.5)*
Vegetation biomass <sup>b</sup>	1.1 (0.1)*	1.5 (0.1)*	1.3 (0.1)	1.4 (0.1)	1.1 (0.1)	1.3 (0.1)
Horizontal depth (cm)	3.6 (0.5)*	6.8 (0.8)*	5.7 (0.6)	5.1 (0.7)	3.7 (0.5)*	5.4 (0.5)*
Maximum grass height (cm)	25.5 (1.7)	31.6 (1.9)	33.2 (1.8)	34.4 (2.4)	26.6 (1.7)	28.3 (1.5)

<sup>a</sup> Total cover (grass, forb, woody).

<sup>b</sup> Vegetation biomass as indexed by visual obstruction readings (Robel et al. 1970).

some individuals traveling 400–600 m. Birds foraging along the foredunes (nearest to the ocean) always moved inland to roost and traveled the greatest distance to roosting sites; there was little overlap between roosting and foraging areas of these birds. The home-range configuration of sparrow #279 illustrates the separation of foraging and roosting locations used by birds in foredune habitat (Fig. 1). Fore-dunes, which sometimes extend no farther inland from the ocean than 100 m, are subject to the harshest environmental conditions on the island. Movement inland by roosting Savannah Sparrows is likely an attempt to escape exposure to the persistent winds coming off the Gulf of Mexico and to find appropriate roosting microhabitat.

Savannah Sparrows, the dominant winter sparrows on the island, foraged in open areas either as solitary individuals or as members of loosely spaced aggregations of conspecifics. Open areas likely provide easier access to available resources. These birds also foraged in areas with higher seed abundance than randomly selected locations, suggesting that they may cue in on resource abundance. Grzybowski (1982, 1983) also found individual and loose aggregations of Savannah Sparrows foraging in areas with low vegetation height and density. Although he did not examine Savannah Sparrows specifically, he found a positive relationship between avian density and seed abundance. Variation in the abundance of wintering emberizid sparrows has been linked to seed production in southeastern Arizona (Pulliam and Brand 1975, Dunning and

Brown 1982). We predicted that foraging areas would be smaller where abundance and biomass of seeds were greater. The lack of a negative relationship suggests that factors other than seed abundance—such as proximity to the coast, the distribution of suitable foraging and roosting patches, or predator avoidance— influence winter home-range size and may also influence the variation observed in Savannah Sparrow movements. The small sample size (nine birds) also may have contributed to the lack of an observed relationship.

Savannah Sparrows foraged in open areas within a matrix of open areas and denser vegetation. This was evident from the greater vegetative biomass at random points compared with that of foraging sites within individual home ranges. Other studies report that wintering Savannah Sparrows forage in open areas adjacent to cover, and suggest that nearby vegetative cover may offer protection from predators (Pulliam and Mills 1977, Watts 1991). This has also been reported for other wintering sparrow species (Lima 1990, Lima and Valone 1991). The foredune habitat used by some sparrows on Padre Island is especially patchy, and may be attractive as foraging habitat, despite the longer distances between foredunes and roosting sites.

Savannah Sparrow roosting sites were often interspersed within or around foraging locations (Fig. 1), and they had greater total cover than foraging and random sites. Greater horizontal vegetation depth at roost sites may be important because it provides space for birds to roost and move under the vegetation with-

out being exposed. Although temperatures rarely dip below freezing in south Texas, frequent winter storms and winds coming off the Gulf Coast likely affect the energy expenditure of roosting individuals. As a result, sparrows roost in areas that provide greater protection from climatic factors, and individuals foraging close to the coast travel farther inland to roost. Other studies of roost-site selection suggest that individuals select sites with the greatest microclimate protection (Kendeigh 1960, Gottfried and Franks 1975, Gyllin et al. 1976, Buttemer 1985). Greater cover could serve to reduce predation risk and provide increased protection from exposure, thus reducing overnight energy expenditure (Walsberg and King 1980). We were able to approach roosting Savannah Sparrows within 1 m, but we were unable to determine the exact proximity of individuals roosting in aggregations. It was apparent, however, that some individuals roosted close together. The mean number of birds roosting in close proximity to each other was low (<5 sparrows), but variation was high. We sometimes observed as many as 30 sparrows roosting in close proximity, suggesting that Savannah Sparrows may derive a benefit from communal roosting, such as reduced predation risk or energy conservation. Other avian species also roost in aggregations during the winter months (Walsberg 1990, Heinrich 2003). With the exception of studies on species that form large communal roosts, studies of nonbreeding passerines have generally disregarded roosting behavior and roost-site selection, often with the assumption that diurnal movement patterns encompass the roosting areas. Our study shows that the distribution of foraging and roosting habitat influences movement patterns and overall home-range size; Savannah Sparrows often roost outside of their foraging areas, and they have specific habitat requirements for foraging and roosting locations.

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